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# Ecomorphology: key to the identity of the White-bearded Greenbul *Criniger ndussumensis*

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**L'écomorphologie : la clé pour identifier le Bulbul de Reichenow *Criniger ndussumensis*.** Le Bulbul de Reichenow *Criniger ndussumensis* des forêts de Basse Guinée et du bassin du Congo ressemble tellement au Bulbul à barbe blanche *C. calurus* sympatrique qu'il est difficile de distinguer les deux espèces, aussi bien sur le terrain qu'en main. *C. ndussumensis* est toutefois plus proche du Bulbul à barbe jaune *C. olivaceus* de Haute Guinée, qui possède un chant et une morphométrie très similaires, y compris un bec plus étroit, bien qu'il présente aussi quelques différences de plumage. *C. olivaceus* a une façon distinctive de chercher sa nourriture, glanant des invertébrés de l'écorce des troncs et des branches, ce qui est jamais observé chez des populations sympatriques de *C. calurus*. Les pattes de *C. olivaceus* possèdent une conformation anatomique particulière, avec des ongles longs et fortement arqués, ce qui constitue apparemment une adaptation à son habitude de s'agripper à l'écorce. Les mensurations confirment que *C. ndussumensis* et *C. olivaceus* sont très similaires en ce qui concerne la morphologie des pattes et la forme du bec, et que les deux espèces diffèrent de façon significative de *C. calurus* par ces deux caractéristiques. Ainsi, la combinaison des ongles longs avec un bec étroit caractérise *C. ndussumensis*, tandis que des ongles courts et un bec large sont diagnostiques pour *C. calurus* ; ces caractéristiques permettent une identification sûre en main. Les différences dans la morphologie des pattes impliquent que la seule espèce en Basse Guinée et le bassin du Congo capable de s'agripper à l'écorce est *C. ndussumensis* et que *C. calurus* en est incapable, *contra* d'innombrables rapports dans la littérature. D'autres caractères, de nature morphologique, comportemental et écologique, par lesquels les deux espèces diffèrent l'une de l'autre sont passés en revue et examinés, et l'attention est attirée sur un cri distinctif, apparemment unique à *C. ndussumensis*. Sur le terrain, ces espèces se distinguent le plus facilement par le comportement, le chant, le cri et la couleur des sous-caudales, cannelle pâle chez *C. ndussumensis*, jaune chez *C. calurus*, bien que ce dernier caractère ne soit pas entièrement fiable. L'auteur n'a pas trouvé de différences dans la couleur des lores, malgré les affirmations du contraire qui ont été publiées. Cette étude réfute également les mentions dans la littérature concernant des individus intermédiaires ou des hybrides entre *C. ndussumensis* et *C. calurus* dans certaines parties du Congo-Kinshasa oriental.

**Summary.** The White-bearded Greenbul *Criniger ndussumensis* of the Lower Guinea and Congo Basin forests is so similar in appearance to the sympatric Red-tailed Greenbul *C. calurus* that separating them in the field or hand is difficult. *C. ndussumensis* is, however, more closely related to the Yellow-bearded Greenbul *C. olivaceus* of Upper Guinea, from which it differs in aspects of plumage, but resembles closely in song and in morphometrics, including sharing a narrower bill. *C. olivaceus* shows distinctive scansorial foraging behaviour, gleaning food from the bark of trunks and branches, something which is unrecorded in sympatric populations of *C. calurus*. *C. olivaceus* is shown here to have modifications to the structure of its feet, including long, strongly curved claws, inferred to be related to its scansorial behaviour. Measurements also show that *C. ndussumensis* exactly resembles *C. olivaceus* in foot morphology and in bill shape, and that they differ significantly in both characters from *C. calurus*. Thus, a combination of long claws and narrow bills characterise *C. ndussumensis* whilst short claws and wide bills are diagnostic of *C. calurus*, features which enable unambiguous determination in the hand. The differences in foot morphology imply that the only species capable of bark-clinging behaviour in Lower Guinea and the Congo Basin is *C. ndussumensis* and that *C. calurus* cannot do so, *contra* numerous literature reports. Other characters, morphological, behavioural and ecological, by which the two species differ are reviewed and assessed, and attention is drawn to a distinctive call, apparently unique to *C. ndus-*

*sumensis*. In the field the most reliable means of separation are behaviour, song, call and the colour of the undertail-coverts, pale cinnamon in *C. ndussumensis*, yellow in *C. calurus*, although this latter character is not wholly reliable. No differences in the colour of the lores were found despite statements to the contrary. This study also refutes reports in the literature of intergrades or hybrids between *C. ndussumensis* and *C. calurus* in parts of eastern Congo-Kinshasa.

The bearded greenbuls are a natural and distinctive group, readily separated from other African bulbuls (Pycnonotidae) by their eponymous beards—their white or yellow throat feathering is long, lax and frequently puffed out in conspicuous display. For long they were thought to be most closely related to a number of similar-looking Asian species, with which indeed they were united in the genus *Criniger*. Molecular studies (Pasquet *et al.* 2001, Moyle & Marks 2006) have, however, recently confirmed what Hall & Moreau (1970) had suggested, that these similarities are superficial only and the two groups are in fact quite distinct. As a result, the Asian species have been transferred to *Alophoixus* whilst the remaining taxa are retained in *Criniger*, now an exclusively African genus, largely confined to the lowland forests of Upper and Lower Guinea and the Congo Basin (Hall & Moreau 1970, Inskipp *et al.* 1996, Sibley & Monroe 1990, Pasquet *et al.* 2001, Fishpool & Tobias 2005). If, however, the genus is well defined, there has been less agreement on the number of species within it.

The recent prevailing trend has been to recognise five: Western Bearded Greenbul *Criniger barbatus*, Eastern Bearded Greenbul *C. chloronotus*, Red-tailed Greenbul *C. calurus*, White-bearded Greenbul *C. ndussumensis* and Yellow-bearded Greenbul *C. olivaceus* (Sibley & Monroe 1990, Keith 1992, Dickinson 2003, Sinclair & Ryan 2003, Fishpool & Tobias 2005, Clements 2007). Of these, *C. calurus* is the most widely distributed, extending from Sierra Leone to Uganda. Three subspecies are conventionally recognised: *verreauxi* in the west, from south-west Senegal to south-west Nigeria, nominate (with which *verreauxi* perhaps intergrades) from south Nigeria to south-west Congo-Kinshasa, and *emini* from west Congo-Kinshasa to Uganda and north-west Tanzania. The other members of the genus are now treated as forming two species-pairs whose distributions largely coincide. Thus, *C. barbatus* of the Upper Guinea forests (with *ansorgeanus* of the Niger Delta region of Nigeria as a subspecies—a treatment, it should be noted,

which merits review) is replaced by the monotypic *chloronotus* in the Cross River area of south-east Nigeria, from where it extends east across the Congo Basin to western Uganda. Although *chloronotus* has, in the past, often been treated as a subspecies of *barbatus*, they were shown by Chappuis (1975) to differ sufficiently in voice as to warrant separation at the species level. These two are not considered further here. Of the remaining monotypic pair, *C. olivaceus* is patchily distributed from eastern Sierra Leone to south-west Ghana whilst *C. ndussumensis* is found across the Congo Basin and Lower Guinea forests, extending west to south-east Nigeria, although its western limit is not well known. Greater uncertainty has, however, attached to its taxonomic position and status.

This study, confirming and developing some ideas first suggested in a neglected paper by Field (1979), seeks to shed light on the relationships between *C. ndussumensis* and *C. olivaceus* and, especially, between *C. ndussumensis* and *C. calurus*, which continue to be confused owing to similarities in their appearance. In particular, it is here shown conclusively that there are consistent differences in bill morphology between *C. calurus* and *C. ndussumensis*, a disputed issue, as well as in foot structure, pointed out long ago but since forgotten, and which I believe to be related to differences in their foraging behaviours. By contrast, *C. ndussumensis* is shown exactly to resemble *C. olivaceus* in foot and bill shape whilst, tellingly, *C. olivaceus* is known to be a specialist at gleaning from the bark of tree trunks and branches. This implies that *C. ndussumensis* should also exhibit similar scansorial foraging behaviour, whereas one might expect that *C. calurus* would not.

Other characters by which *C. ndussumensis* is reported to be separable from *C. calurus* are reviewed and reconsidered, based upon both museum studies of specimen material by the author and on personal observations of birds in the field and in the hand while participating in avifaunal survey work in and around Cross River National Park, Oban Division, south-east Nigeria

in December 2004. As a result, *C. ndussumensis* is confirmed to have a call, hitherto largely overlooked, which is apparently unique to it, recorded from neither *C. calurus* nor *C. olivaceus*. The differences in bill and foot structure, allied with a number of plumage characters, mostly relatively minor or subtle and some not wholly reliable, will enable the accurate identification of *C. calurus* and *C. ndussumensis* in the hand and, combined with differences in voice and behaviour, should do so, in most cases, in the field.

A brief description of the principal features of the appearance of the three species is called for. Thus, nominate *calurus* has a dark grey-brown head and neck, whilst the rest of the upperparts are olive-green, except for the rufous uppertail-coverts and tail. The throat is white, the flanks and breast-sides, together with a narrow band across the upper breast, are dark olive whilst the remainder of the breast, belly and undertail-coverts are bright yellow. The rather larger western race *verreauxi* differs principally in having the uppertail-coverts and tail olive-green, which are hence concolorous with the rest of the upperparts. The eastern race *emini*, the smallest, is to some extent intermediate in coloration since its uppertail-coverts and tail are dull olive-rufous and are therefore poorly contrasting. This summary applies, however, almost equally well—see below—to *C. ndussumensis* and therein lies the problem. In Upper Guinea, separation of *C. calurus verreauxi* from *C. olivaceus* is straightforward since the latter has a yellow, not a white, throat and a green (except for a limited area in the centre of the belly), not a yellow, breast and belly. The uppertail-coverts and tail are also green and in this it therefore resembles the sympatric *C. calurus verreauxi*.

### Background to the problem

Gyldenstolpe (1923, 1924) gave the name *Trichophorus swainsoni bannermani* to six specimens collected in the Semliki Valley area of eastern Congo-Kinshasa that differed 'from the races of *Trichophorus calurus* by having a shorter and considerably weaker bill'—*Trichophorus* is now treated as a synonym of *Criniger* (although Oberholser (1905) makes the case that, in fact, *Criniger* should be considered the junior synonym of *Trichophorus*!). For one of these races, the one which he said occurred alongside *bannermani* in the Semliki Valley, Gyldenstolpe used the name *T.*

*calurus ndussumensis*. Chapin (1948, 1953) pointed out that the type of *C. ndussumensis*, described by Reichenow in 1904, and collected from within 40 km of the type locality of *T. swainsoni bannermani*, was in fact also slender-billed and that therefore the latter was a junior synonym of the former. He, however, disputed whether the slender billed *C. ndussumensis* did co-exist in the Semliki Valley with a thicker billed form, stating that there 'most' were 'strikingly slender-billed' (Chapin 1948). For the thicker billed population, which he said occupied 'most of the Upper Congo Forest and many wooded areas in Uganda', he coined the name *Criniger calurus emini* and considered that *ndussumensis*, which he treated as another subspecies of *calurus*, was largely restricted to the Semliki, and parts of the Rutshuru, valleys (Chapin 1948, 1953).

Shortly thereafter, Berlioz (1954, 1955), on the basis of birds collected in Gabon, concluded that the slender- and stout-billed forms could in fact occur side by side and therefore represented two species. Furthermore, Berlioz (1955) pointed out that the slender-billed birds, for which he used the name *Criniger (?swainsoni) bannermani* in one place and ?*C. swainsoni* in a second, had rather stronger legs and longer toes than the stout-billed birds, which he called *C. calurus*. White (1956) agreed with Berlioz that two species were involved but declared that the name *swainsoni* could not be used for the slender-billed form since it was a junior synonym of *verreauxi*, the (thick-billed) Upper Guinea race of *C. calurus*. He went on to say that the slender-billed form resembled closely *C. olivaceus* of the Upper Guinea forests in bill structure and stated that Berlioz's specimens therefore 'must be called *C. o. ndussumensis*', but was unable to 'see much difference in the feet despite what Berlioz has written on this' (White 1956). The following year, Serle (1957) went further and, on the basis of measurements of a large series of skins of *C. calurus calurus* from Nigeria and Cameroon, concluded there were no differences in dimensions of either bill or leg to indicate that more than one species was involved, nor was there any 'consistent inverse correlation between the size of the digits and the bill', *contra* Berlioz (1954, 1955). He, however, measured bill length and depth, *not* width, and remarked that accurate measurement of digits on skins was not possible. Next to comment were Rand (1958) and Rand *et al.* (1959),

who contradicted Serle regarding bill shape differences but did not mention either legs or feet. Subsequently, in light of the observations of White (1956) and Rand (1958), Serle (1965) re-examined a more extensive series from Nigeria and Cameroon and, while conceding that they were indeed separable into stout- and slender-billed groups, retained them all under the heading *C. calurus calurus* and remained unconvinced that 'the two groups are biologically separated'. He, however, apparently considered closed the matter of leg and foot size for he did not to return it.

Despite Serle's lack of conviction, there has been little subsequent disagreement—Eisentraut (1973) is an exception—as to *C. ndussumensis* and *C. calurus* being specifically distinct, even if (reputedly) impossible to tell apart unless in the hand. The issue of whether to treat *ndussumensis* as a species in its own right or as a subspecies as *C. olivaceus*, as White (1956, 1962) had proposed, has nonetheless continued. Thus, while Prigogine (1971), Mackworth-Praed & Grant (1973), Chappuis (1975, 2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993) and Christy & Clarke (1994) consider *ndussumensis* a subspecies of *olivaceus*, Hall & Moreau (1970), Lippens & Wille (1976), Keith (1992), Borrow & Demey (2001) and Fishpool & Tobias (2005), for example, all treat them as separate species.

### Other characters

In addition to bill size and shape, other characters by which *C. ndussumensis* has been reported to differ from *C. calurus* include a more distinct, greyish-white ante-ocular spot; greyer, less brown, crown, more extensively dusky olive flanks and breast; less well-developed nuchal hairs and rictal bristles and, finally, cinnamon or buffy, rather than yellowish, undertail-coverts. These characters are reported variously by White (1956), Rand (1958), Rand *et al.* (1959) and Serle (1965), and most are repeated in subsequently published handbooks and field guides. It is readily apparent that none of these is particularly striking; a study of skins suggests that neither, with the possible exceptions of rictal bristle length and strength of nuchal hairs, is infallible.

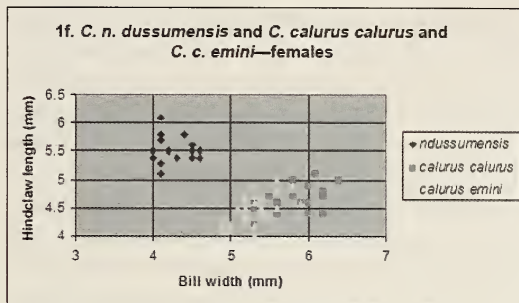
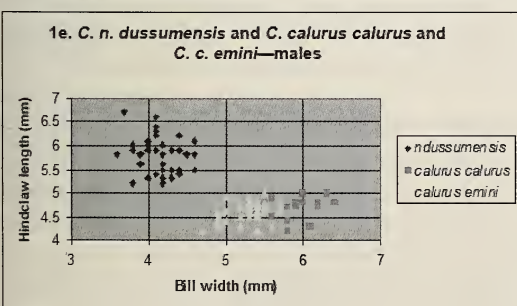
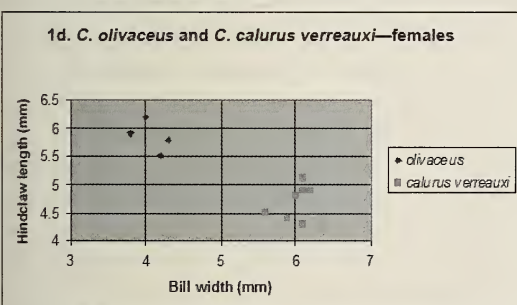
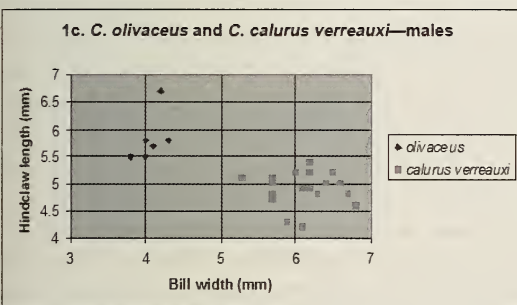
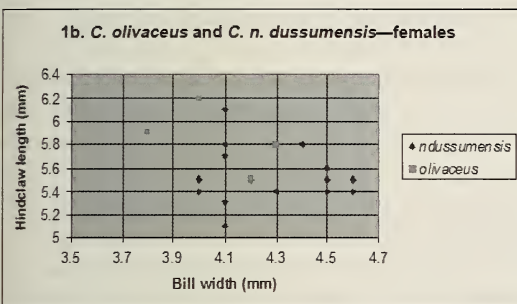
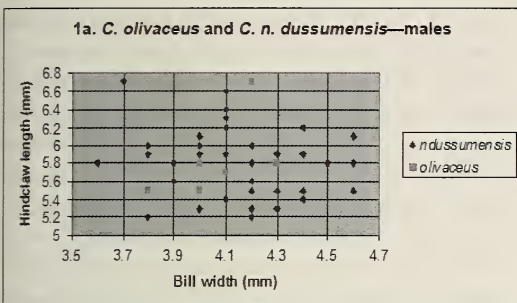
The most reliable means of separating the two species in the field has hitherto proved to be song, for, although similar, there are consistent differences between them which are diagnostic. Thus,

the song of *C. calurus* consists of a cheerful, rising *chup-chup-chwirulup*, whereas that of *C. ndussumensis* is a harsh, evenly pitched *whut-chruw-chruw*, which lacks the former's cheerful, sprightly quality (Dowsett-Lemaire & Dowsett 1991, Keith 1992, Christy & Clarke 1994, Chappuis 2000, Borrow & Demey 2001). It is notable that the song of *C. olivaceus* is indistinguishable (or almost so—see section on Voice below) from that of *C. ndussumensis*, and indeed Chappuis (2000) demonstrated that the former can be provoked into song and aggressive display by playback of the voice of the latter, something which has been confirmed by others (E. Dowsett-Lemaire *in litt.* 2008). This has been advanced as further evidence of the close affinity between the two and, indeed, of their conspecificity (Chappuis 1975, 2000, Dowsett & Dowsett-Lemaire 1993).

In addition, in the east of its range, where sympatric with *C. calurus emini*, *C. ndussumensis* often also differs from it in having a more rufous, as opposed to a greenish, tail. This indeed was one of the distinguishing characters mentioned in the type description (Gyldenstolpe 1923) and was reaffirmed by Chapin (1948, 1953), who considered that the combination of a reddish tail and uppertail-coverts plus a narrow bill was diagnostic of *C. ndussumensis*, whilst a greenish tail and a broad bill typified *C. calurus emini*. Inspection of specimen material, identified on the basis of bill and foot morphology, reveals however that there is sufficient variation in tail colour of both *C. ndussumensis* and *C. calurus emini* for it not to be reliable as a distinguishing feature; the only *consistent* character difference between them then known, as Field (1979) noted, was in fact bill width, but of this Chapin (1948, 1953) was unaware. This misunderstanding has given rise to incorrect reports of intergrades and hybrids between the two—see below.

### Ecomorphology—resolution of the problem

The point of departure for trying to resolve the confusion between *C. calurus* and *C. ndussumensis* lies, as was pointed out by Field (1979), in the situation that pertains in the Upper Guinea forests. Here, *C. calurus verreauxi* occurs alongside *C. olivaceus*. As mentioned above, the latter, with a yellow throat and olive-green breast and flanks, is readily distinguishable from the white-throated, yellow-bellied *C. calurus verreauxi*. *C. olivaceus* is



**Figure 1.** Scatter plots of hindclaw length against bill width (mm) of allopatric *Criniger olivaceus* and *C. ndussumensis* males (a) and females (b), to show similarities, and of *C. olivaceus* and *C. calurus verreauxi* males (c) and females (d) (sympatric in Upper Guinea) and *C. ndussumensis*, *C. calurus calurus* and *C. calurus emini* males (e) and females (f) (sympatric in Lower Guinea and Congo Basin), to show differences.

Position relative de la longueur de l'ongle de l'orteil postérieur contre la largeur du bec (en mm) des espèces allopatriques *Criniger olivaceus* et *C. ndussumensis* mâles (a) et femelles (b) pour présenter leurs ressemblances, et de *C. olivaceus* et *C. calurus verreauxi* mâles (c) et femelles (d) (sympatriques en Haute Guinée) et *C. ndussumensis*, *C. calurus calurus* et *C. calurus emini* mâles (e) et femelles (f) (sympatriques en Basse Guinée et dans le bassin du Congo), pour présenter les différences.

further distinguished by its behaviour; to quote Field (1979) '... food is obtained by searching the trunks and branches of trees, the birds clinging in an almost nuthatch-like manner, peering into crevices and even investigating the undersides of branches'. In the region, this foraging behaviour is unique to *C. olivaceus*, never having been recorded for *C. calurus verreauxi* (Field 1979, Fishpool *et al.* 1994, Gatter 1997, Borrow & Demey 2001, Fishpool & Tobias 2005). The method commonly used by *C. calurus verreauxi* is to snatch invertebrate prey from leaves (often from the under-surfaces) and, more rarely, to take berries in hovering flight from perches on thin branches and stems, often horizontally oriented (Field 1979, Gatter 1997, Fishpool & Tobias 2005). Both are conspicuous elements of mixed foraging parties, although *C. calurus* is usually much the more common (see below).

Given that *C. olivaceus* is a specialist at clinging to vertical surfaces and overhangs, one might expect this to be reflected in foot structure, since it is known that birds which forage in this manner show a number of associated morphological adaptations. These include the possession of relatively

longer and more curved claws, in order to be able to cling more effectively to vertical surfaces, than birds—such as *C. calurus verreauxi*—which do not (Richardson 1942, Bock & Miller 1959, Norberg 1986). From this it follows they should differ in the dimensions of the foot, whilst it might be expected that *C. olivaceus* and *C. ndussumensis*, given their presumed close relationship, should not. One would also expect the other two races of *C. calurus* to resemble *verreauxi* in foot morphology.

In order to test this—mindful of the comments of Berlioz (1954, 1955) regarding leg and foot structure—and also to confirm whether there are indeed differences in bill shape between the races of *C. calurus* on the one hand and *C. olivaceus* and *C. ndussumensis* on the other, a series of skins were measured using calipers. Measurements were made of bill length (to skull) and width at the distal end of the nostrils (immediately anterior to the thread often used in skins to tie together the two mandibles), and the length of the hindclaw, from the mid-point—generally the lowest—of the distal toe pad to the claw tip. While Serle's (1957) remark, mentioned above, concerning the difficulty of measuring toes on skins is certainly largely correct, it is possible to measure claw length accurately on most specimens. The claw on the hallux, as well as being the largest in all cases, was also often found to be the most readily accessible.

The results of these measurements are presented in Table 1 and in Fig. 1 as scatter plots of claw length against bill width. Data are presented separately for males and females since, for all members of the genus, males average larger than females in standard measurements (Keith 1992, Fishpool & Tobias 2005). The results show the close correspondence between *C. olivaceus* and *C. ndussumensis* in hindclaw length and bill width in both sexes (Fig. 1a, b); t-test statistics confirm there to be no significant difference in either character in males, nor for bill width in females (Table 1). There is a difference in hindclaw length in females, significant at the 5% level, which may be attributable to the small sample size of *C. olivaceus* (Table 1). Between *C. olivaceus* and *C. calurus verreauxi*, however, there are considerable differences in both parameters, with *C. olivaceus* conspicuously longer clawed and narrower billed; there is no overlap in the range of either metric and the differences are highly significant (Table 1, Fig. 1c, d).

Moreover, *C. ndussumensis* differs similarly, and as significantly, from both *C. calurus calurus* and *C. calurus emini* (Table 1, Fig. 1e, f). Although in *C. calurus emini* the ranges of hindclaw length in females and of bill width in males approach their equivalents in *C. ndussumensis*, there is again no overlap. Only in hindclaw length of female *C. calurus calurus* is there a minimal amount of overlap with female *C. ndussumensis*; the longest clawed *C. calurus calurus* and the shortest clawed *C. ndussumensis* (one specimen of each) both measured 5.1 mm.

Overall, therefore, *C. olivaceus* and *C. ndussumensis* resemble each other closely in size of hindclaw and in bill width, and both differ consistently from all races of *C. calurus* in these parameters. Table 1 and Fig. 1 also show that the three races of *C. calurus* are similar in proportions of hindclaw length and bill width, although in the smallest race, *C. calurus emini*, bill width averages rather narrower (a difference not reflected in hindclaw length). Figs. 2 and 3 illustrate the differences between *C. calurus* and *C. ndussumensis* and, for claw length, the similarity between *C. ndussumensis* and *C. olivaceus*.

Bill length data (tip to skull) are also presented in Table 1 and show, for *C. ndussumensis* and *C. olivaceus*, extensive overlap in their ranges in both sexes and no significant difference between females, whilst bills in male *C. olivaceus* were found to average rather shorter, a difference significant at the 5% level, perhaps again explicable by the small sample of *C. olivaceus* available. By contrast, there are strongly significant differences between *C. olivaceus* and *C. calurus verreauxi*, and between *C. ndussumensis* and both *C. calurus calurus* and *C. calurus emini*, with *C. calurus calurus* having longer bills in all cases. While, however, the ranges of *C. olivaceus* and *C. calurus verreauxi* differ considerably and there is little overlap between *C. ndussumensis* and *C. calurus calurus*, with *C. ndussumensis* and *C. calurus emini*, the smallest of the three races, the overlap is extensive.

### Other morphological characters

Of the other reported morphological character differences between *C. calurus* and *C. ndussumensis* mentioned above, the most consistent appears, from an examination of large series of museum skins, to be the development of the rictal bristles. Although no quantitative assessments were

attempted, the bristles of *C. calurus* seemed to be consistently longer and more robust, probably related to differences in their foraging strategies. Thus, in *C. ndussumensis* they extend only weakly beyond the distal edge of the nares and, at most, appear no longer or thicker than a human eyelash, whereas the bristles of *C. calurus* often extend strongly beyond the nares, up to three-quarters the length of the bill, with the largest conspicuously more robust than a human eyelash (Figs. 2 and 4).

It is also probable that *C. calurus* may have consistently longer, thicker, more robust nuchal hairs or filoplumes than *C. ndussumensis*; these long, bristle-like feathers on the neck, a feature of the genus, are of unknown function. Again, while

no attempt was made to quantify this difference, superficial examination did suggest that while equally numerous as those of *C. calurus*, in *C. ndussumensis* they often appeared shorter, narrower and more flexible.

More conspicuous both in the museum tray and the field are the undertail-coverts which, in the majority of *C. calurus*, are the same sulphur yellow colour, or almost so, as the breast and belly, whilst in most *C. ndussumensis* they are cinnamon or buffy and therefore contrast with the yellow belly and breast (Fig. 4). This contrast is readily apparent in the field (pers. obs.). Unfortunately, examination of skin material suggests this distinction is not infallible; three of 75 *C. ndussumensis*

**Table 1.** Comparative measurements of length of hindclaw and width and length of bill of three *Criniger* species. Hindclaw measured from lowest point of distal toe pad to claw tip, bill width at distal edge of nares, bill length from tip to skull.

Comparison of allopatric *C. olivaceus* and *C. ndussumensis* to show similarity, and comparisons of *C. olivaceus* and *C. calurus verreauxi* (sympatric in Upper Guinea) and of *C. ndussumensis* with both *C. calurus calurus* and *C. calurus emini* (sympatric in Lower Guinea and the Congo Basin) to show differences. Results of two-tailed Student's t-test shown, where n.s. indicates not significant, \* indicates significance at 5% level and \*\* at 1% level. Data for sexes presented separately since males average larger than females in standard measurements. Data for unsexed specimens are omitted. All measurements by the author.

**Tableau 1.** Mensurations comparatives de la longueur de l'ongle de l'orteil postérieur et de la largeur et la longueur du bec de trois espèces de *Criniger*. L'ongle de l'orteil postérieur a été mesuré à partir du point le plus bas jusqu'au bout de l'ongle, la largeur du bec entre les points les plus éloignés des narines, la longueur du bec de son bout jusqu'au crâne. Les espèces allopatriques *C. olivaceus* et *C. ndussumensis* ont été comparées afin de faire ressortir leurs ressemblances ; la comparaison de *C. olivaceus* et *C. calurus verreauxi* (sympatriques en Haute Guinée) et de *C. ndussumensis* avec *C. calurus calurus* et *C. calurus emini* (sympatriques en Basse Guinée et dans le bassin du Congo), met en évidence leurs différences. Les résultats du test bilatéral de Student sont présentés ; n.s. = pas significatif, \* = significatif au niveau de 5% et \*\* au niveau de 1%. Les données des mâles et des femelles sont présentées séparément, car les premiers sont en moyenne plus grands que les dernières en ce qui concerne les mensurations standards. Les données de spécimens dont le sexe n'avait pas été établi ont été omises. Toutes les mensurations ont été prises par l'auteur.

|                             | Range   | Hindclaw     |    |    | t-test differences | Range        | Bill width  |    |  | t-test differences | Range         | Bill length |    |  |
|-----------------------------|---------|--------------|----|----|--------------------|--------------|-------------|----|--|--------------------|---------------|-------------|----|--|
|                             |         | Mean ± s.e.  | n  |    |                    |              | Mean ± s.e. | n  |  |                    |               | Mean ± s.e. | n  |  |
| <b>Males</b>                |         |              |    |    |                    |              |             |    |  |                    |               |             |    |  |
| <i>C. ndussumensis</i>      | 5.5–6.7 | 5.79 ± 0.057 | 41 |    | 3.6–4.6            | 4.15 ± 0.037 | 43          |    |  | 17.9–20.5          | 19.19 ± 0.129 | 33          |    |  |
| <i>C. olivaceus</i>         | 5.5–6.7 | 5.83 ± 0.153 | 7  | ns | 3.8–4.3            | 4.06 ± 0.061 | 7           | ns |  | 18.0–19.1          | 18.59 ± 0.162 | 7           | *  |  |
| <i>C. olivaceus</i>         | 5.5–6.7 | 5.83 ± 0.153 | 7  |    | 3.8–4.3            | 4.06 ± 0.061 | 7           |    |  | 18.0–19.1          | 18.59 ± 0.162 | 7           |    |  |
| <i>C. calurus verreauxi</i> | 4.2–5.4 | 4.9 ± 0.07   | 19 | ** | 5.3–6.8            | 6.12 ± 0.095 | 18          | ** |  | 20.7–24.7          | 22.74 ± 0.252 | 18          | ** |  |
| <i>C. ndussumensis</i>      | 5.5–6.7 | 5.79 ± 0.057 | 41 |    | 3.6–4.6            | 4.15 ± 0.037 | 43          |    |  | 17.9–20.5          | 19.19 ± 0.129 | 33          |    |  |
| <i>C. calurus calurus</i>   | 4.2–5.0 | 4.73 ± 0.05  | 20 | ** | 5.4–6.4            | 5.9 ± 0.06   | 20          | ** |  | 20.4–23.9          | 22.39 ± 0.175 | 20          | ** |  |
| <i>C. calurus emini</i>     | 4.2–5.0 | 4.61 ± 0.038 | 31 | ** | 4.7–5.7            | 5.26 ± 0.047 | 31          | ** |  | 17.8–21.9          | 19.95 ± 0.15  | 30          | ** |  |
| <b>Females</b>              |         |              |    |    |                    |              |             |    |  |                    |               |             |    |  |
| <i>C. ndussumensis</i>      | 5.1–6.1 | 5.54 ± 0.054 | 18 |    | 4.0–4.6            | 4.25 ± 0.048 | 19          |    |  | 17.4–19.9          | 18.7 ± 0.182  | 16          |    |  |
| <i>C. olivaceus</i>         | 5.5–6.2 | 5.8 ± 0.109  | 6  | *  | 3.8–4.3            | 4.13 ± 0.08  | 6           | ns |  | 17.2–19.6          | 18.6 ± 0.364  | 6           | ns |  |
| <i>C. olivaceus</i>         | 5.5–6.2 | 5.8 ± 0.109  | 6  |    | 3.8–4.3            | 4.13 ± 0.08  | 6           |    |  | 17.2–19.6          | 18.6 ± 0.364  | 6           |    |  |
| <i>C. calurus verreauxi</i> | 4.3–5.1 | 4.7 ± 0.113  | 7  | ** | 5.9–6.2            | 6.01 ± 0.067 | 8           | ** |  | 20.6–22.3          | 21.41 ± 0.258 | 7           | ** |  |
| <i>C. ndussumensis</i>      | 5.1–6.1 | 5.54 ± 0.054 | 18 |    | 4.0–4.6            | 4.25 ± 0.048 | 19          |    |  | 17.4–19.9          | 18.7 ± 0.182  | 16          |    |  |
| <i>C. calurus calurus</i>   | 4.2–5.1 | 4.66 ± 0.051 | 20 | ** | 5.3–6.4            | 5.85 ± 0.075 | 20          | ** |  | 19.5–24.0          | 20.94 ± 0.278 | 20          | ** |  |
| <i>C. calurus emini</i>     | 4.0–5.0 | 4.50 ± 0.049 | 28 | ** | 4.9–5.9            | 5.30 ± 0.048 | 28          | ** |  | 17.9–20.9          | 19.49 ± 0.17  | 27          | ** |  |

specimens were considered to have yellow or yellowish undertail-coverts while, of 134 *C. calurus*, 13, involving all three subspecies, were recorded as gingery or 'gingery?'. Although this assessment was complicated because the process of skin preparation appeared to have resulted in some discoloration of the feathering around the ventral region of a number of specimens, and that at least two of the *C. calurus* specimens scored as gingery were clearly juveniles (of which this colour may be a feature—Keith (1992) reported a 'very young' *C. calurus emini*, still with some downy feathers, as having 'undertail-coverts ochre', and this is also true of skins of the nominate race of a similar age examined in the Natural History Museum (NHM), Tring, UK, it seems clear that this difference is not absolute.

The same is true of the extent of olive-green on the flanks and breast-band; in *C. ndussumensis* the olive on the flanks and across the breast tends to be more extensive with correspondingly less yellow on the lower breast and belly (Fig. 4) but some skins are indistinguishable from *C. calurus* in this respect. There does seem to be a slight but seemingly consistent—although I did not systematically check a large series—difference in crown colour, with that of *C. ndussumensis* being greyer than *C. calurus*, in which it is rather brown-

er and warmer, but this must be hard, if not impossible, to detect in the field.

Finally, I could find no difference in the colour of the lores; the presence of a larger, more contrasting greyish-white ante-ocular spot in *C. ndussumensis* was first reported by White (1956) and repeated, sometimes with a caveat, by a number of other authors (Rand 1958, Rand *et al.* 1959, Hall & Moreau 1970, Keith 1992, Christy & Clarke 1994, Borrow & Demey 2001, Sinclair & Ryan 2003), but I have been unable to detect such a difference either in the museum or, more significantly, in live birds in the hand. During field work in the proposed extension to Cross River National Park (CRNP), Oban Division, Nigeria, east of Old Ndebiji village (c.05°35'N 08°50'E) in December 2004, an area where *C. ndussumensis* was encountered frequently, I was able to watch a number at close range on several occasions as well as to examine birds caught in mist-nets. Two *C. ndussumensis* captured and photographed—bill width of both at distal end of nostrils 4.3 mm—had the orbit of the eye and the lores sparsely feathered whitish grey, under which blue-grey skin could be seen, contrasting somewhat with the surrounding darker grey feathering of the head and giving the bird a rather spectacled appearance (Fig. 5).

**Table 2.** Character differences between *Criniger ndussumensis* and *C. calurus calurus* and *C. calurus emini*. Corresponding data also given for *C. olivaceus* but not all differences between it and the others are shown. Ranges of measurements for both sexes combined.

**Tableau 2.** Différences entre les caractères de *Criniger ndussumensis* d'une part et *C. calurus calurus* et *C. calurus emini* d'autre part. Les données correspondantes de *C. olivaceus* sont incluses, mais les différences entre cette espèce et les autres ne sont pas toutes présentées. Les mensurations des deux sexes ont été combinées.

|                                    | <i>C. ndussumensis</i>  | <i>C. c. calurus</i> and <i>C. c. emini</i>  | <i>C. olivaceus</i>                       |
|------------------------------------|---|--|---|
| Bill width at distal edge of nares | Narrow, 3.6–4.6 mm  | Wide, 4.7–6.4 mm   | Narrow, 3.8–4.3 mm                        |
| Hindclaw length                    | Long, 5.1–6.7 mm  | Short, 4.0–5.1 mm  | Long, 5.5–6.7 mm                          |
| Rictal bristles                    | Relatively short and slender                                      | Relatively long and stout  | Relatively short and slender              |
| Filoplumes                         | Relatively short and slender                                      | Relatively long and stout  | Relatively short and slender              |
| Crown                              | Olive grey-brown, colder  | Olive-brown, warmer  | Olive-green                               |
| Flanks                             | Broadly dark olive-green  | Dark olive-green may be more confined, with yellow of belly more extensive                               | Dark olive-green                          |
| Undertail-coverts                  | Usually pale cinnamon or buffy, contrasting with belly and breast | Usually sulphur yellow or dirty yellow, contrasting little or not at all with breast and belly           | Dark olive-green, tinged buffy            |
| Upper tail                         | Rufous but may be duller, more olive in east of range             | Rufous (nominate), dull olive-rufous ( <i>emini</i> ). [Green in <i>C. c. verreauxi</i> ]                | Green                                     |
| Foraging behaviour                 | Scansorial; clings to branches and trunks                         | Non-scansorial   | Scansorial; clings to branches and trunks |
| Song                               | Harsh, level <i>whut-chrur-chrur</i>                              | Cheerful, lively, rising <i>chup-chup-chwirulup</i>  | Harsh <i>whut-chrur-chrur</i>             |
| Call                               | <i>querg-querg, trur-trur</i>                                     | <i>tyip-tyip</i>   | ?   |
| Social unit                        | Pairs or small family parties                                     | Small or, frequently, large groups   | Pairs or small family parties             |
| Habitat                            | Good-quality evergreen forest                                     | Good-quality and more degraded evergreen forest, semi-evergreen forest, riparian forest and even thicket | Good-quality evergreen forest             |



However, *C. calurus* has an extremely similar face pattern, the main difference being that the spectacled effect is more pronounced, both by the slightly more contrasting browner tones of the surrounding head feathering, and because the sparsely feathered peri-orbital area appears to be wider (pers. obs.; see also the photograph and line drawing in Brosset [1971] and the line drawing in Keith [1992]). These features are of course not apparent in skin preparations.

### Voice

The field work in CRNP, Oban, also enabled me to confirm that a commonly heard call, often uttered in shorter or longer series and which I transliterated variously as *querg-querg*, *querk-querk-querk* or *queg-queg*, was made by *C. ndussumensis*, for not only were these calls made by birds which foraged on tree trunks in the manner described above, but also one bird of the pair caught in the mist-net mentioned above obligingly uttered a single, soft *querg* as I approached. This call is, in fact, included on Chappuis (2000) as the second cut of the *C. ndussumensis* recording as 'song and calls, March, Ngotto Forest, Gabon [in error for Central African Republic] P. Christy'. Françoise Dowsett-Lemaire (*in litt.* 2008) has confirmed that she is familiar with this call from south-east Nigeria, Cameroon and Congo-Brazzaville, and indeed refers to it in Dowsett-Lemaire and Dowsett (1991) where it is transliterated as 'trur'. In addition, what appears to be the same call is ascribed to *C. ndussumensis* by Christy & Clarke (1994) and rendered *prrrreuk prrrreuk prrrreuk*. Also present in the same area of CRNP was *C. calurus calurus* and its well-known call, variously rendered *tyip-tyip*, *peeyu*, *peeyu*, *kiu*, *kiu* and *piih*, *piih* (Keith 1992, Christy & Clarke 1994, Chappuis 2000, Borrow & Demey 2001, Fishpool & Tobias 2005; Dowsett-Lemaire & Dowsett 1991 present a sonogram), was frequently heard, as were the songs of both species, which appear on Chappuis (2000).

Although, as noted above, the song of *C. ndussumensis* is very similar to that of *C. olivaceus* of Upper Guinea, F. Dowsett-Lemaire (*in litt.* 2008) has pointed out that it is not, in fact, identical. In *C. olivaceus* the last note is not a monotonous *kerrur* as it is in *C. ndussumensis*, but is modulated in frequency. This is apparent on a close listening to recordings on Chappuis (2000) where the song

of *C. ndussumensis* can also be heard to consist of two or three notes, whereas in *C. olivaceus* it comprises four, albeit the first is very short. In the field, however, one often hears just the three notes so it is possible this first note is not always included (F. Dowsett-Lemaire *in litt.* 2008). As mentioned above, however, these differences are not sufficient to prevent *C. olivaceus* reacting to playback of the song of *C. ndussumensis*.

### Ecological requirements and social behaviour

There are differences too between *C. ndussumensis* and *C. calurus* in both their habitat preferences and social behaviour. Thus, *C. ndussumensis* (and, indeed, *C. olivaceus*) are largely restricted to tall-canopy primary and mature secondary evergreen rain forest, and hence are usually absent from degraded, secondary habitats, open canopy, semi-evergreen forest, gallery forest etc. *C. calurus* is, on the other hand, less specialised and thus more tolerant of disturbed forest types, including edges of clearings and even overgrown gardens, as well as occurring in drier forests including riverine thicket habitats (Dowsett-Lemaire & Dowsett 1991, Fishpool & Tobias 2005; F. Dowsett-Lemaire *in litt.* 2008). As a result, *C. calurus* is more geographically widespread in areas of overlap than both *C. ndussumensis* and *C. olivaceus*.

Moreover, where the two species co-occur, *C. calurus* is almost always more numerous than *C. ndussumensis* (Rand 1958, Prigogine 1971, Dowsett-Lemaire & Dowsett 1991). An explanation for this is provided by Dowsett-Lemaire & Dowsett (1991) and F. Dowsett-Lemaire (*in litt.* 2006) who point out that *C. ndussumensis* is almost invariably seen or caught in mist-nets in territorial pairs or, at most, together with one or two immatures; by contrast, the social unit of *C. calurus* is usually larger, such that five or six are regularly seen together, while, occasionally, groups may number at least twice that many. The situation is similar in Upper Guinea where *C. olivaceus*, like *C. ndussumensis*, occurs in pairs or small family parties, not in large groups.

The features by which *C. ndussumensis* can be separated from *C. calurus* are summarised in Table 2. Overall, in the field, birds showing scansorial behaviour are *C. ndussumensis*, and can be further distinguished by vocalisations and, rather less reliably, by coloration of undertail-coverts and of the flanks. In the hand, individuals with a combina-

tion of long hindclaws ( $\geq 5.1$  mm) and narrow bills ( $\geq 4.6$  mm) are *C. ndussumensis* whilst birds with short hindclaws ( $\leq 5.1$  mm) and wide bills ( $\geq 4.9$  mm) are *C. calurus*, either nominate or *emini*.

## Discussion

Given that *C. ndussumensis* differs consistently and significantly from sympatric races of *C. calurus* in claw length and bill shape, while exactly resembling *C. olivaceus* in these characters, it is reasonable to infer that *C. ndussumensis* shares the same foraging strategy and scansorial behaviour as *C. olivaceus* and, equally, that all races of *C. calurus*, lacking the requisite adaptations, are unlikely to be able to forage in this way. There are, however, numerous statements in the literature, relating to Lower Guinea and the Congo Basin, which aver that *C. calurus* does glean food from the bark of trunks and branches or that both species do so, such that they are therefore indistinguishable in behaviour. Examples include Chapin (1953) [already pointed out by Field (1979) as more likely attributable to *C. ndussumensis*], Brosset (1971), Lippens & Wille (1976), Brosset & Erard (1986), Dowsett-Lemaire & Dowsett (1991), Keith (1992), Sargeant (1993), Christy & Clarke (1994) and Sinclair & Ryan (2003). While I do not mean to suggest that *C. calurus*, a generalist feeder, does not occasionally snatch prey from tree bark by sally-gleaning and hovering or take food items from bark that it can reach while perched, nor that *C. ndussumensis* must necessarily feed exclusively from tree bark, I believe that reports that *C. calurus* exhibits scansorial behaviour should be treated with caution; I consider it much more likely that they refer to *C. ndussumensis* and to *C. ndussumensis* alone.

This confusion has meant, and continues to mean, that other information provided by these authors cannot be unequivocally attributed to either species. In particular, Brosset & Erard (1986) state that although they caught, collected or ringed birds 'on several occasions' with the characteristics of *C. ndussumensis*, they explicitly refer all their observations to *C. calurus*, as they were unable to separate them in the field using either voice or behaviour. An explanation for this has been provided by F. Dowsett-Lemaire (*in litt.* 2008) who reports a conversation she once had with A. Brosset, the author of the bulbul accounts in Brosset & Erard (1986), in which he acknowl-

edged that since he was tone deaf, he was, to his great sorrow, unable to distinguish between them. From the descriptions of foraging behaviour, in which they say '*C. calurus*' resembles a woodpecker rather than a bulbul, it is apparent however that they were indeed regularly encountering *C. ndussumensis* and therefore the value of their data on population densities, breeding, food etc. is reduced as it must be a mix of observations of the two species. In other field studies the same identification difficulties have led authors to be explicit about the uncertainty as to which species their observations refer—see for example Bowden (1986) and Rodewald *et al.* (1994).

Even though the advent of knowledge of the songs of *C. calurus* and *C. ndussumensis*, with their relatively subtle but diagnostic differences (Chappuis 1975, Dowsett-Lemaire & Dowsett 1991), helped considerably in field identification of the two species and has become recognised as the most effective means of distinguishing between them, confusion has persisted.

Although there is no doubt that *C. calurus* is responsible for the *kiu* or *tyip* call and there is unequivocal evidence to link the *querg* call with *C. ndussumensis*, it remains to be established categorically that these calls are exclusive to each species. During field work in CRNP both species were frequently seen in, and both calls commonly heard from, mixed-species flocks but attributing calls to individual, identifiable birds under such conditions was often not feasible; however, when pairs or small groups of birds were encountered separately, they were heard to make only the one type of call. This supports the observations of Dowsett-Lemaire & Dowsett (1991) who state that the *kiu* call is made by *C. calurus* alone and of Christy & Clarke (1994), mentioned above, who associate one call exclusively with each species. I suspect therefore that Dowsett-Lemaire & Dowsett (1991) are correct in saying that the two species share only an alarm-call, *tchic*. As a result, I am doubtful that the third recording attributed to *C. ndussumensis* on Chappuis (2000) and annotated 'another type of call? (identification not certain) July, Korup National Park, SW Cameroon, P. Rodewald' was in fact made by that species since it sounds to me more like a slight variant of the *kiu* call of *C. calurus*.

It is intriguing that the *querg-querg* call of *C. ndussumensis* has not been recorded for *C. oli-*

*vaceus*; this call is unreported in Upper Guinea (Fishpool *et al.* 1994, Borrow & Demey 2001; R. Demey pers. comm.; pers. obs.). This is all the more curious given the similarity in their songs, as mentioned above.

It should be noted that although hindclaw length has been used in this analysis, this is only one of a number of possible metrics, and not necessarily the most appropriate, that could have been used to assess differences in foot morphology. It was however the one found most feasible in museum specimens. Thus, in addition to length, the degree of curvature of the hindclaw—the claw arc—could have been measured (differences between the claw arcs of both *C. ndussumensis* and *C. olivaceus* from those of *C. calurus* are readily apparent in Fig. 3, where it also appears that the claw tips of *C. ndussumensis* and *C. olivaceus* are sharper and more pointed). I also believe that Berlioz (1954, 1955) was correct in stating that *C. ndussumensis* has longer, narrower toes than *C. calurus*, a view which is supported by the images shown in Fig. 6. I am not however persuaded that the two differ in tarsal size, *contra* Berlioz. Notches in the distal toe pads, reported to be a feature of certain climbing passerines (Clark 1973), were not found in *C. ndussumensis* or *C. olivaceus*.

The validity of the contrasting loreal spot as a diagnostic character in *C. ndussumensis* has been questioned before. Thus, Friedmann & Williams (1971) noted that four specimens with 'fairly greyish' lores from their series of 35 from Bwamba, Uganda, did not have 'particularly narrow bills' while one that had a bill 'as narrow as any [of Rand's loaned specimens of] *C. ndussumensis*' did not have grey on the lores. Sargeant (1993) and Bowden (2001) also found the loreal spot unreliable as a distinguishing feature.

An illustration of the observation, mentioned above, that across much of its range, *C. ndussumensis* is considerably less common than *C. calurus*, attributable to the latter being both more widespread and usually occurring at higher densities, is provided by the relative number of skins in museums; thus, NHM, Tring has 25 *C. ndussumensis* and 106 *C. calurus calurus* and *C. calurus emini*, while comparable figures for the Field Museum of Natural History, Chicago and the Royal Museum for Central Africa (RMCA), Tervuren, Belgium are 15 vs. 92 and 23 vs. >400, respectively.

Chapin, in his 1948 description of *Criniger calurus emini*, wrote of 'intergradation between *C. ndussumensis* and *emini*', reporting it 'in specimens taken 46 kilometers south of Irumu and at Angumu, 190 kilometers west of Lake Edward' and, later, he (Chapin 1953) referred to the specimen from near Irumu as a 'thin-billed example of *emini*' whilst of the Angumu material he noted that of '13 specimens of *C. calurus* . . . nine agree with *emini*, but four have bills virtually as slender as those of *C. ndussumensis*. Even these have tails and tail-coverts less rufous, with one possible exception'.

These observations have been repeated by others (e.g. Hall & Moreau 1970, Lippens & Wille 1976) and, in some cases, taken rather further. Thus, Rand (1958), referring to both Chapin's observations and his own examination of the same specimens, refers to 'hybrids', as also does Rand (1960)—who writes that *C. ndussumensis* 'hybridises extensively with *C. calurus emini* in Semliki Valley area'—White (1962) and Keith (1992).

During a visit to the American Museum of Natural History (AMNH), New York, Nigel Collar was able to locate 13 of the 14 specimens to which Chapin (1953) refers. These he kindly examined on my behalf and measured their bill widths and hindclaw lengths. His measurements reveal that, for both characters, seven fall squarely within the ranges of *emini* shown in Table 1 (where these data are not included), while five are equally unequivocally *C. ndussumensis*; the measurement of the hindclaw of the final individual is anomalously small, possibly as a result of damage, and is well outside the range of both. The bill width however suggests it to be *C. ndussumensis*. The colour of the upper tail of all specimens was noted as dull olive-rufous. The anomalous specimen aside, these findings therefore demonstrate that there is no 'intergradation' between *C. calurus emini* and *C. ndussumensis* in the Semliki Valley area; in consequence, there is nothing to suggest that *C. ndussumensis* and *C. calurus emini* behave as anything other than separate species in this part of their range, as elsewhere. These observations further confirm that tail colour is unreliable as a distinguishing character, as well as providing independent verification of the utility of the bill and claw metrics in diagnosing *C. calurus emini* and *C. ndussumensis*.

As a final point, the English vernacular names currently in use for the species of this genus are

particularly unsatisfactory and confusing. Thus, White-bearded Greenbul for *C. ndussumensis*, as used by Keith (1992), Borrow & Demey (2001), Sinclair & Ryan (2003) and Fishpool & Tobias (2005), has been used by Serle *et al.* (1977) and others for *C. calurus*, while *C. barbatus* is equally white-bearded. *C. calurus* is now usually called Red-tailed Greenbul, e.g. by Keith (1992), Dowsett & Forbes-Watson (1993), Borrow &

Demey (2001), Sinclair & Ryan (2003) and Fishpool & Tobias (2005), but this is only really applicable to the nominate race, the tail in the other races being green or greenish, whilst many other bulbuls, including *C. ndussumensis*, have red or reddish tails which contrast with the back and wings. The earlier name Thick-billed Red-tailed Greenbul of Mackworth-Praed & Grant (1973), is little better, and neither indicates that the bird is a

#### Captions to photos on opposite page

**Figure 2.** Dorsal views of bills of *Criniger calurus emini* (left) and *C. ndussumensis* (right) illustrating differences in width. Also apparent are the longer, more robust rictal bristles in *C. calurus*. Left-hand specimen no. 58585, male, Congo-Kinshasa; right-hand specimen no. 31984, male, Cameroun. Background scale in mm. (L. D. C. Fishpool, © Royal Museum for Central Africa, Tervuren, Belgium)

Vue dorsale des becs de *Criniger calurus emini* (à gauche) et *C. ndussumensis* (à droite) illustrant la différence en largeur. Les vibrisses plus longues et robustes de *C. calurus* sont également bien visibles. Spécimen de gauche no. 58585, mâle, Congo-Kinshasa; spécimen de droite no. 31984, mâle, Cameroun. Échelle en mm. (L. D. C. Fishpool, © Musée Royal de l'Afrique Centrale, Tervuren, Belgique)

**Figure 3.** From top to bottom: lateral views of hindclaws of *Criniger calurus calurus*, *C. calurus emini*, *C. ndussumensis* and *C. olivaceus* illustrating differences between the upper and lower pairs in length and curvature. Upper specimen no. 1902.7.15.10 male, Cameroon, NHM, Tring; upper middle specimen no. 67257, female, Congo-Kinshasa, RMCA, Tervuren; lower middle specimen no. 1911.5.31.355, male, Cameroon, NHM, Tring; bottom specimen no. 1930.12.17.44, female, Guinea, NHM, Tring. Background scale in mm. (L. D. C. Fishpool, top and lower two © The Natural History Museum, Tring; upper middle specimen © Royal Museum for Central Africa, Tervuren, Belgium)

De haut en bas : vue latérale de l'ongle de l'orteil postérieur de *Criniger calurus calurus*, *C. calurus emini*, *C. ndussumensis* et *C. olivaceus* illustrant la différence en longueur et courbure entre les paires du haut et du bas. Spécimen du haut no. 1902.7.15.10, mâle, Cameroun, NHM, Tring ; deuxième spécimen du haut no. 67257, femelle, Congo-Kinshasa, MRAC, Tervuren ; deuxième spécimen du bas no. 1911.5.31.355, mâle, Cameroun, NHM, Tring ; spécimen du bas no. 1930.12.17.44, femelle, Guinée, NHM, Tring. Échelle en mm. (L. D. C. Fishpool, spécimen du haut et les deux du bas © The Natural History Museum, Tring ; le quatrième © Musée Royal de l'Afrique Centrale, Tervuren, Belgique)

**Figure 4.** Ventral views of *Criniger calurus calurus* (top) and *C. ndussumensis* showing more buffy undertail-coverts and more extensively olive-green flanks in *C. ndussumensis*. The slenderer bill and weaker rictal bristles of *C. ndussumensis* are also apparent. Upper specimen no. CG.1954.65, female, Gabon; lower specimen no. CG.1955.456, female, Gabon. (L. D. C. Fishpool, © Muséum National d'Histoire Naturelle, Paris)

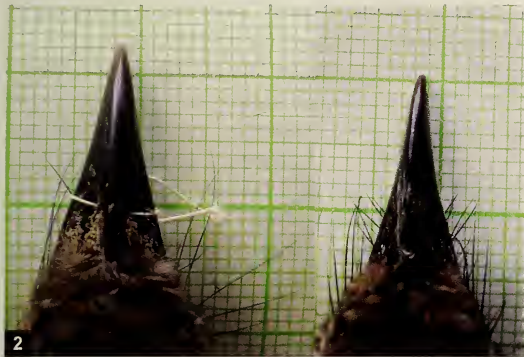
Vue ventrale de *Criniger calurus calurus* (en haut) et *C. ndussumensis* illustrant les sous-caudales plus roussâtres et les flancs au vert-olive plus étendu de *C. ndussumensis*. Le bec plus fin et les vibrisses moins longues de *C. ndussumensis* sont également visibles. Spécimen du haut no. CG.1954.65, femelle, Gabon ; spécimen du bas no. CG.1955.456, femelle, Gabon. (L. D. C. Fishpool, © Muséum National d'Histoire Naturelle, Paris)

**Figure 5.** *Criniger ndussumensis*, east of Old Ndebiji, Nigeria, in proposed extension to Cross River National Park, Oban Division, 9 December 2004. Identification based, amongst other things, upon vocalisation of individual in mist-net and bill width of 4.3 mm at distal end of nostrils (see text). Sexed as male on presence of cloacal protuberance. (L. D. C. Fishpool)

*Criniger ndussumensis*, à l'est de Old Ndebiji, Nigeria, dans l'extension proposée du Parc National de Cross River, Division d'Oban, 9 décembre 2004. Identification basée, entre autres, sur les vocalisations de l'oiseau dans le filet japonais et la largeur du bec ( 4,3 mm) entre les points les plus éloignés des narines (voir texte). Déterminé comme mâle sur la base de la présence d'une protubérance cloacale. (L. D. C. Fishpool)

**Figure 6.** Dorsal views of anterior portions of feet of *Criniger c. calurus* (left) and *C. ndussumensis* (right) illustrating differences in toe length. Left-hand specimen no. 1902.15.10, male, Cameroon; right-hand specimen no. 1947.90.61, Nigeria, male. (L. D. C. Fishpool, © The Natural History Museum, Tring)

Vue dorsale de la partie antérieure des pattes de *Criniger c. calurus* (à gauche) et *C. ndussumensis* (à droite) illustrant les différences en longueur des orteils. Spécimen de gauche no. 1902.15.10, mâle, Cameroun ; spécimen de droite no. 1947.90.61, Nigeria, mâle. (L. D. C. Fishpool, © The Natural History Museum, Tring)



bearded greenbul. Similarly, Yellow-bearded Greenbul for *C. olivaceus*, as used by Keith (1992), Borrow & Demey (2001), Sinclair & Ryan (2003) and Fishpool & Tobias (2005), as well as Yellow-throated Olive Greenbul of Mackworth-Praed & Grant (1973), do not satisfactorily distinguish it from the equally yellow-bearded *C. barbatus*. Dowsett & Forbes-Watson (1993) use White-

bearded Greenbul for the yellow-throated *C. olivaceus* because they treat *C. ndussumensis* as a race of it.

I therefore offer the following alternative vernaculars which are unambiguous, more accurate and more informative:

- C. barbatus* . . . Western Greater Bearded Greenbul
- C. chloronotus* . . . Eastern Greater Bearded Greenbul
- C. calurus* . . . Lesser Bearded Greenbul
- C. olivaceus* . . . Western Slender Bearded Greenbul
- C. ndussumensis* Eastern Slender Bearded Greenbul

These better indicate both the coherence of the genus and their relative sizes and distributions, whilst the epithet slender for *C. olivaceus* and *C. ndussumensis* reflects their more gracile bills and feet.

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